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Size distribution and reproductive phenology of the invasive Burmese python (*Python molurus bivittatus*) in the Greater Everglades Ecosystem, Florida, USA

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Abstract

The design of successful invasive species control programs is often hindered by the absence of basic demographic data on the targeted population. Establishment of invasive Burmese pythons (*Python molurus bivittatus*) in the Greater Everglades Ecosystem, Florida USA has led to local precipitous declines (> 90%) of mesomammal populations and is also a major threat to native populations of reptiles and birds. Efforts to control this species are ongoing but are hampered by the lack of access to and information on the expected biological patterns of pythons in southern Florida. We present data from more than 4,000 wild Burmese

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pythons that were removed in southern Florida over 26 years (1995–2021), the most robust dataset representing this invasive population to date. We used these data to characterize Burmese python size distribution, size at maturity, clutch size, and seasonal demographic and reproductive trends. We broadened the previously described size ranges by sex and, based on our newly defined size-stage classes, showed that males are smaller than females at sexual maturity, confirmed a positive correlation between maternal body size and potential clutch size, and developed predictive equations to facilitate demographic predictions. We also refined the annual breeding season (approx.100 days December into March), oviposition timing (May), and hatchling emergence and dispersal period (July through October) using correlations of capture morphometrics with observations of seasonal gonadal recrudescence (resurgence) and regression. Determination of reproductive output and timing can inform population models and help managers arrest population growth by targeting key aspects of python life history. These results define characteristics of the species in Florida and provide an enhanced understanding of the ecology and reproductive biology of Burmese pythons in their invasive Everglades range.

Keywords
clutch size, ecological timing, Everglades National Park, gonadal development, invasive species, morphometrics, oviposition, reproductive potential, reptile, size at maturity, snake

Introduction

Invasive species cause some of the most ecologically damaging and costly impacts on ecosystems (Fantle-Lepczyk et al. 2022). They can outcompete and consume natives, impacting species across trophic levels. Invasive reptiles, and snakes in particular, comprise some of the most infamous species with documented deleterious trophic impacts in multiple systems. For example, the invasive brown treesnake (*Boiga irregularis*) in Guam's tropical ecosystem has decimated native vertebrate populations on the island, driving many to extirpation or extinction (Savidge 1987; Wiles 1987; Rodda and Fritts 1992), and leading to seed dispersal loss and potential changes in forest structure (Rogers et al. 2017). Recently, the common wolf snake (*Lycodon capucinus*) has been linked to the precipitous decline of lizard species on Christmas Island, AUS (Emery et al. 2021). In continental USA, the invasive Burmese python (*Python molurus bivittatus*) has been linked to severe declines of mammalian prey populations and the accompanying ecological impacts in southern Florida's Greater Everglades Ecosystem (Dorcas et al. 2012; Hoyer et al. 2017; Burkett-Cadena et al. 2021; Taillie et al. 2021). The success of Burmese pythons is likely due, in part, to their size coupled with their reproductive biology (Willson et al. 2011; Card et al. 2018). Though some work has been done describing instances of python demographics and reproduction across its invasive range in southern Florida (Snow et al. 2007b; Krysko et al. 2008), stronger inferences can be made with increased sample sizes, particularly from the wild population.

The vast landscape and inaccessible habitats of the Greater Everglades Ecosystem paired with extremely low detection probabilities of the Burmese python (est. < 5%; Nafus et al. 2020) have stymied the accumulation of robust, long-term ecological and biological data of the species. These large predatory snakes may have been introduced

to, and established in, Everglades National Park by the mid-1980's or even earlier (Willson et al. 2011). Since then, the species has spread across the entire southern portion of Florida and has been implicated in severe population declines of some mid-sized mammals in the area (Dorcas et al. 2012; McCleery et al. 2015), as well as in changes to vector-borne disease transmission dynamics (Hoyer et al. 2017; Burkett-Cadena et al. 2021), food-web perturbations (Reichert et al. 2017), and spillover of parasites to native species (Miller et al. 2018). However, little is known about much of the Burmese pythons' biology or reproductive phenology in the wild (but see Krysko et al. 2012; Smith et al. 2015). Several detection and removal strategies have been tested and/or implemented over the years (e.g., Reed et al. 2011; Hunter et al. 2015; Falk et al. 2016; Parker et al. 2021), but captures remain low, and population-level information or temporal trends remain limited. However, understanding this species' morphology and reproduction in its entire invasive range which spans southern Florida will provide researchers with a demographic baseline which can aid in the development of new, biologically targeted control tools.

To determine if control efforts are effective, an invasive species' population size needs to be estimable so that measured changes can be documented. Population abundances and survival changes across ontogeny can be estimated using predictive mathematical tools such as stage (size or age class) structured population matrix models (Hanley et al. 2019a) using basic data on phenotypic and reproductive parameters. Yet, for Burmese pythons, no long-term or robust reproductive stage data exist, and the basic questions about population dynamics or growth potential in the wild (e.g., Hanley et al. 2019b; Currylow et al. 2022a) are almost completely unknown. Additionally, inconsistent methods across studies and over time exacerbate issues with defining species size-stage classes through size at maturity or identifying phenotypic variation (Feldman and Meiri 2012). For example, snake studies often measure animal body size using total length (tip of snout to tip of tail; e.g., Burger et al. 1987; Snow et al. 2007b) while others use snout-vent length (SVL; tip of snout to vent; e.g., Reed et al. 2016; Josimovich et al. 2021). This difference is important to note when attempting to understand or compare morphologies between the sexes because male squamates store their hemipenes, inverted, in the ventral tail base, causing males to have generally longer tails (and therefore relatively longer total lengths) than females of the same SVL (Fitch 1960; Shine et al. 1999).

Our objectives were to characterize size at maturity, reproductive status, and temporal trends in wild Burmese python populations distributed within the Greater Everglades Ecosystem. We compiled 26 years of data on a variety of morphometrics collected from more than 4,000 python captures resulting from several invasive species removal efforts and studies across southern Florida between 1995 and 2021 (Currylow et al. 2022b). With these data we aimed to address the following hypotheses: if wild Burmese pythons 1) exhibit sexual dimorphism, then females will be larger than males at sexual maturity; 2) have clutch sizes that depend on maternal body sizes, then large clutches will be associated with larger body sizes; 3) synchronously hatch and disperse from nests, then they will appear on the landscape en masse within one

period; and 4) exhibit a regular annual reproductive cycle, then gonadal states of each sex will uniformly differ across months. We were able to use this data compilation to describe morphologies and gonadal states, define size distributions, develop predictive size equations, characterize size-stage classes, identify reproductive status, and infer reproductive potential (size at maturity and potential clutch size). We also investigated those data across time to better understand the seasonality of reproductive trends and hatchling emergence in southern Florida, USA.

Methods

Study site

Our study site included private, state, and federal lands in Florida where invasive Burmese pythons have established. The area encompasses much of the Greater Everglades Ecosystem in Florida, USA from south of Lake Okeechobee through the Florida Keys. From east to west coasts, southern Florida is surrounded by a complex of roads and man-made waterways. The Everglades is composed of limestone bedrock covered by ridge and slough habitats and mangrove complexes (Lodge 2017). These areas are characterized by freshwater marshes, tree islands, tropical hardwood hammocks, pinelands, cypress forests, mixed and mangrove swamps, prairies, coastal lowlands, and estuarine systems (Lodge 2017).

Specimen acquisition and processing

Burmese python specimens used in this study were sourced year-round through nonprofit organization, Federal, and State funded research, removal, volunteer, and management programs and private individuals between 1995 and 2021 (see citations herein). We report morphometric and/or reproductive information from 4,007 specimens from across southern Florida, many of which were collected on linear features such as roadways and levees (Fig. 1). We recorded location of capture (UTM WGS84), date of capture/death, sex, weight (grams), snout vent length (SVL, cm), tail length (cm), tail completeness (intact or broken/incomplete), total length (cm), reproductive status based on gonad developmental state (see below), and number of most developed ovarian structure/oviductal eggs. To allow for future comparisons of our data to other records, we recorded both SVL and tail length when possible, tested for differences between the sexes, and aimed to provide equations for the estimation of one body size measurement using the other.

Reproductive parameters

We recorded reproductive data for pythons during necropsies and classified reproductive status using a visual assessment of the specimens' most developed gonadal structure

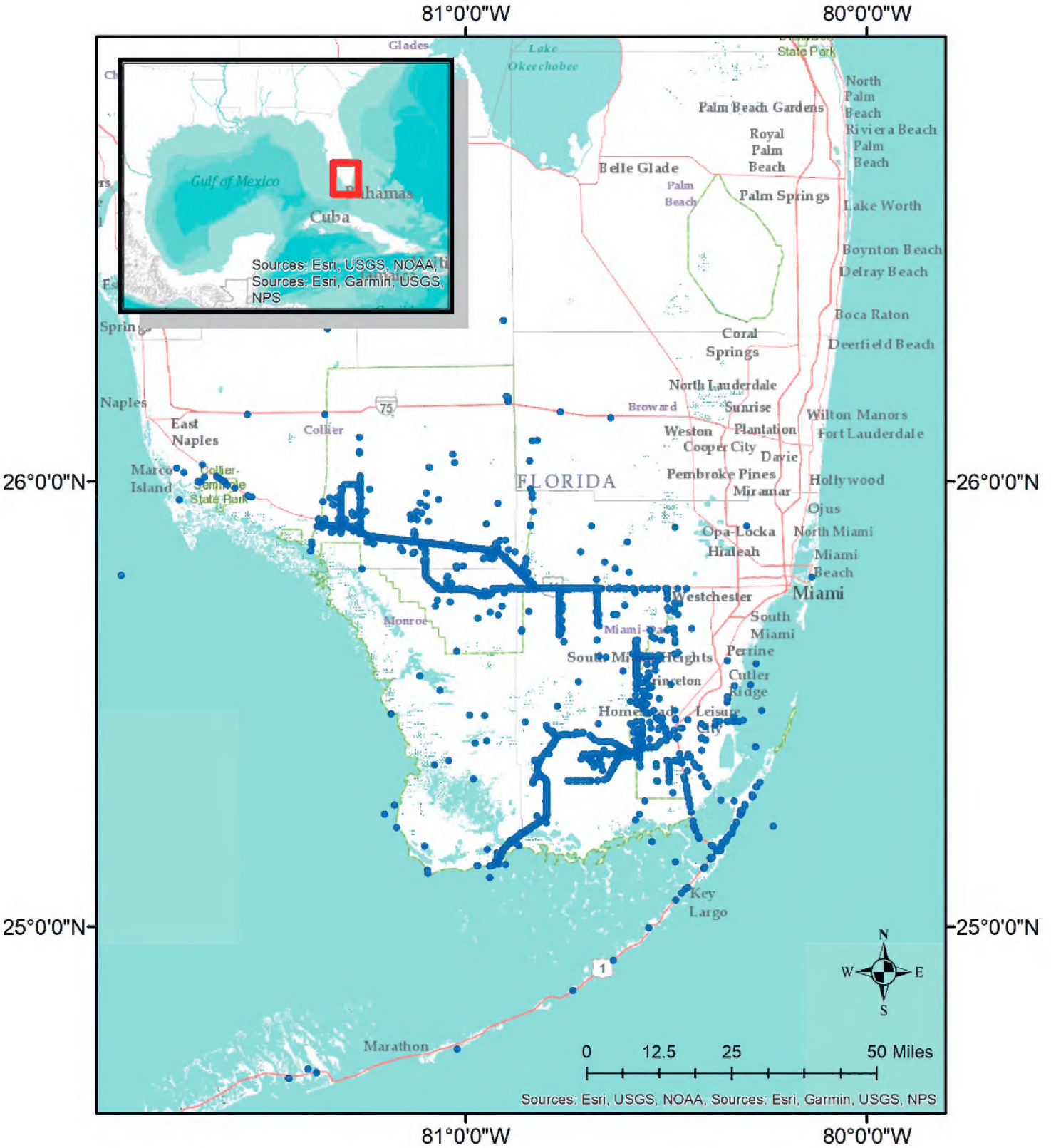

Figure 1. Map of removal locations of 4,007 Burmese python (*Python molurus bivittatus*) specimens concentrated along roadways and levees across southern Florida, USA from 1995 through 2021. The Florida base map was compiled from several data providers, including the U.S. Geological Survey, National Oceanic and Atmospheric Administration, National Park Service, Garmin, and Esri to a scale of ca. 1:70 kilometer (ArcGIS Desktop 10.8.1 version 10.8.1.14362).

(following Aldridge 1979; Seigel et al. 2001). Gonad developmental state categories included: undeveloped (no follicles/oviductal eggs or testes categorized or identified), primary follicles (small, preliminary or pre-vitellogenic oocytes), secondary follicles (pre-ovulatory vitellogenic follicles), oviductal eggs (post-ovulatory/ovigerous), flaccid testes (testes distinguished but not turgid), semi-turgid testes, and turgid testes.

We discovered and report information from 13 Burmese python nests laid between 2006 and 2022. Five of these have been partially described previously (see Snow et al. 2007a; Snow et al. 2010; Hanslowe et al. 2016; Wolf et al. 2016; Currylow et al. 2022c), and we therefore cite those with the comparisons to other nests on oviposition phenology, maternal python SVL, and clutch sizes for summary purposes. In six instances, we discovered and monitored oviposition in wild pythons in the field as part of other studies. Five of the nests were found after hatching and clutch sizes were inferred by counting eggshells.

Statistical analyses

Size distribution

To process the raw dataset for analyses, we grouped and averaged all data from any single animal that was measured multiple times within a single month. Where available, we summarized the median sizes (SVL and weights) of python captures and/or separated pythons by sex. We regressed SVL by weight of each sex and fit a second-degree polynomial to visualize the non-linear relationship with an r-squared value.

Size at maturity

To determine if wild Burmese pythons exhibit sexual size dimorphism where females are larger than males at sexual maturity with the non-normal data, we used the non-parametric Wilcoxon method adjusted for multiple pairwise comparisons to test for mean differences of SVL between stages of gonad developmental state (undeveloped, flaccid testes, semi-turgid testes, turgid testes, primary follicles, secondary follicles, or oviductal eggs). Using the reproductive stages that correlated with size ranges, we then categorized size-stage classes (juvenile, sub-adult, adult) to represent general sizes at maturity for each sex. For those individuals with intact tails, we tested if tail length was proportionally different across size-stage classes using a Standard Least Squares Restricted Maximum Likelihood model (REML) with size-stage class as the predictor variable and the proportion of the tail length to total body length for individuals as the response variable with individual identification as a random effect to account for repeated measures. We then tested if the proportion of tail length to total length was different between the sexes overall, as well as within each size-stage class group using REMLs. To determine predictive equations that could be used to standardize and interpret records across studies, we fit a regression line between tail length and SVL or SVL and total length for each sex for those individuals with intact tails and known sexes.

Clutch size

To determine if wild Burmese pythons have larger clutch sizes as they grow to larger body sizes, we evaluated potential clutch size for correlation with maternal body size

(SVL). We used females having secondary follicles or oviductal eggs at necropsy, enumerating them as a maximum clutch size proxy. We then performed a regression analysis to determine a predictive equation for the relationship. We further investigated if there was a difference in the potential clutch size estimates using only pre-ovulatory secondary follicles vs only oviductal eggs. We again performed regression analyses for each of these potential clutch size estimates to maternal body size to refine predictive equations. For the nests we discovered from 2006 through 2022 that were associated with known females, we regressed female size (SVL) of maternal pythons with the total number of oviposited eggs and fit a linear regression to determine a predictive equation for the relationship.

Seasonal trends

To evaluate if wild hatchling Burmese pythons synchronously hatch and disperse, we investigated seasonality (monthly variation) of morphometric trends (size and reproductive parameters). We used a standard least squares regression model fit with the restricted maximum likelihood method using SVL as the response variable and month as the predictor variable. We included individual python identification as a random effect to account for repeated measures of some individuals. When investigating juvenile python size classes to identify temporal trends in hatching or emergence seasonality, we again used the above-described model but now included weight (g) as a response variable and followed model tests with a least squares means Tukey HSD post hoc analysis to detect significant differences among months. We used a bivariate nonparametric probability density plot to visualize the spread, correlation, and skewness of the annual juvenile size data. We then used the contour polygons to identify the characteristic annual size distinctions within the juvenile size-stage class as young-of-year (YoY; hatchling pythons emerging before calendar-year end) and older juveniles.

To determine if Burmese pythons follow a regular annual reproductive cycle in southern Florida, we modeled adult reproductive cycles of each sex over time using logistic regression. We performed a chi-square test of independence to assess the relationship between gonadal state and observation month to understand annual cycles in gonadal recrudescence (where females' follicles become markedly and heavily vitellogenic and males' testes become engorged and turgid) and regression. For all other analyses where we compared between two groups, we used pooled t-tests or chi squared analyses depending on data type. For analyses where more than two variables were investigated, we used analyses of variance followed by Tukey HSD post hoc analyses where appropriate.

Sample sizes varied across years and for different analyses depending on available data, therefore both year ranges and sample sizes are specified for each figure and analysis. All analyses were carried out using JMP statistical software (SAS Institute Inc 2021) and significance was determined at $\alpha \leq 0.05$. The data used in this manuscript are available as a USGS data release (Currylow et al. 2022b).

Results

We collected necropsy data from every specimen based on specimen condition, staffing, and data needs over the years (1995–2021; Suppl. material 1). Due to the nature of the collection of the dataset, sample sizes for each analysis are stated and may vary based on the data that were collected at the time. Of the 4,007 individual pythons represented in the dataset, 126 were morphometrically remeasured over multiple months (2–19 months) before euthanasia as part of other projects and constitute 487 rows of the 4,378 total data rows on which we report here. All individual animals have only one set of reproductive status (gonadal state) measurements, as those necessitated destructive sampling (i.e., during necropsies). As the dataset reflects opportunistic captures and surrenders, these data may not represent the entirety of the populations' variation or demographic patterns (e.g., Falk et al. 2016).

Size distribution

Burmese pythons for which SVL was recorded ranged in size from 39.6 to 498.0 cm SVL (median = 167 cm, n = 3,938) and 40–84,800 g (median = 3,270 g, n = 4,191). Grouped by sex, females grew to larger sizes ranging 39.6–498.0 cm SVL (median = 165 cm, n = 1,740) and 50–84,800 g (median = 2,768 g, n = 1,765), males ranged 42.0–399.5 cm SVL (median = 173 cm, n = 2,046) and 50–44,000 g (median = 3,800 g, n = 2,212; Fig. 2) and those for which sex was indeterminable or was not recorded ranged 44.7–424.0 cm SVL (median = 62 cm, n = 148) and 40–63,100 g (median = 179 g, n = 214).

Size at maturity

We confirmed that wild Burmese pythons in Florida indeed exhibit sexual dimorphism whereby females are larger than males at sexual maturity, but also that males have longer tails than females of the same size. We found trends in python size (SVL and weight) by gonadal development state (Fig. 3). We subsequently used gonadal development and associated SVLs to identify size differences associated with reproductive status (non-reproductive or reproductively active; Table 1; overall model $F_{6,2117} = 755.1500$, $p < 0.0001$), though some overlap occurs at the extremes or depending on season (see seasonal trends below). The SVLs of reproductive individuals were different between the sexes, where females were longer on average (mean = 297.8 cm SVL, SE = 4.0726, 95% confidence interval (CI) = 285.0–310.5 cm SVL, n = 138) than males (211.0 cm SVL, SE = 2.3882, 95% CI = 206.7–216.1 cm SVL, n = 399; $F_{1,535} = 334.3382$, $p < 0.0001$).

We used sizes associated with gonad developmental state from Table 1 to designate size-stage classes in each sex (Table 2). Primary follicles can be found in adult females throughout the year, but the smallest females with follicles were 151 cm SVL (see Table 1), so those below this threshold were considered juvenile females. Similarly, males may exhibit flaccid testes when not reproductively active, but the smallest males exhibiting semi-turgid testes were 125 cm SVL; males below this length were considered

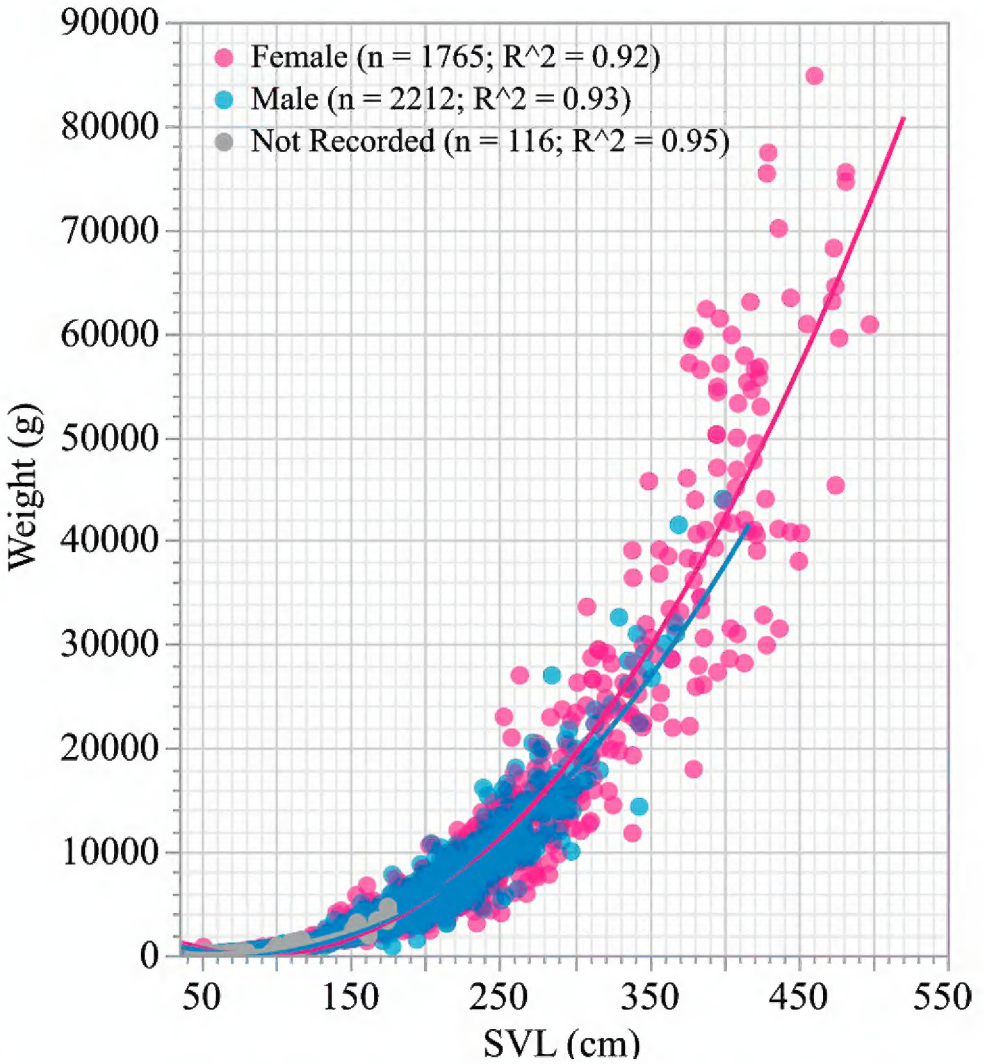

Figure 2. Snout-vent lengths (SVL; cm) of Burmese pythons (*Python molurus bivittatus*) from 1995 through 2021 in southern Florida, USA. Females (magenta) grow larger and longer than males (blue). Individuals without sex recorded (grey) are limited to juvenile and subadult size-stage class for clarity. Second-degree polynomial goodness of fit lines shown by sex with sample sizes and R^2 values in parentheticals.

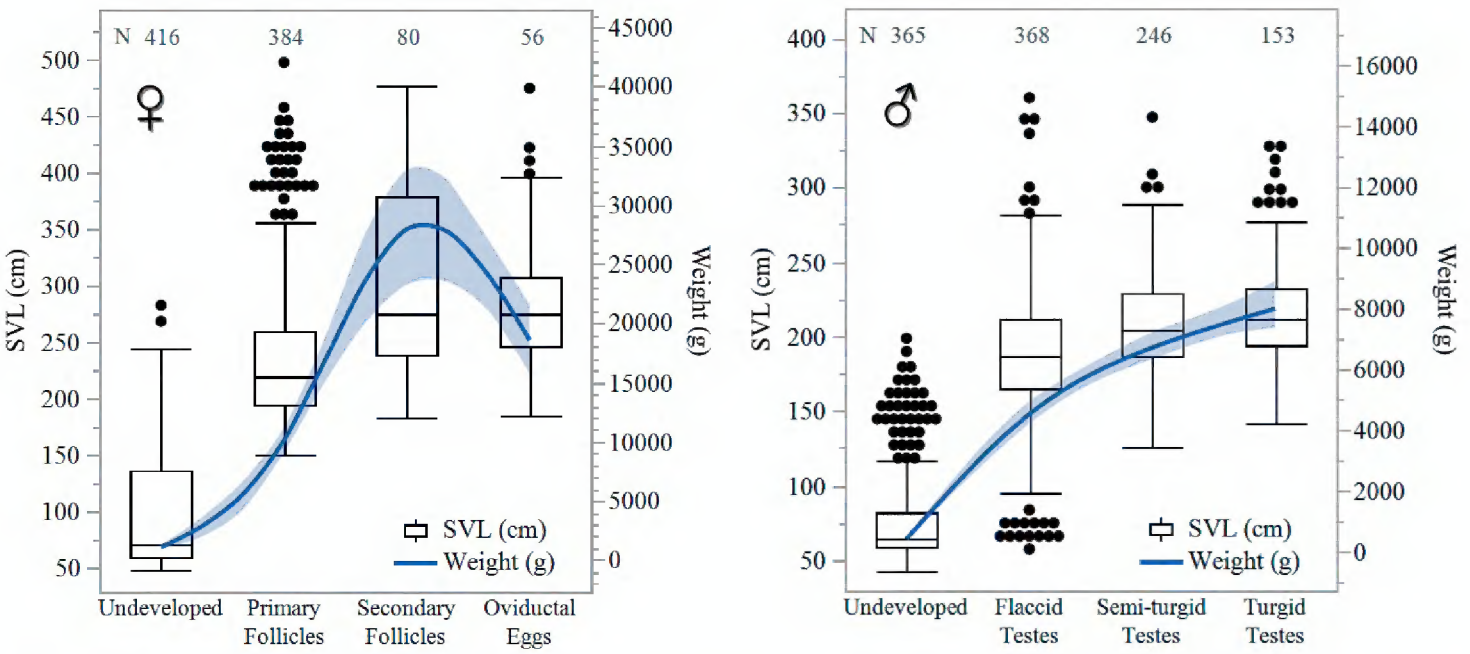

Figure 3. Female (left) and male (right) gonad developmental state by animal size data from necropsied Burmese pythons (*Python molurus bivittatus*) captured from 2003 through 2021 in southern Florida, USA. Snout-vent lengths (SVL, cm) are displayed as boxplots and mean body weights (g) are represented as the solid blue smoother line with 95% confidence buffer; sample sizes are listed across the top. Mean SVLs and weights were highest in pythons with more progressed gonadal development and were different from the smaller-sized pythons with less- or undeveloped gonadal states (see Table 1).

Table 1. Burmese python (*Python molurus bivittatus*) gonad developmental state (testes, follicles, or oviductal eggs) by quantiles of snout-vent lengths (SVL, cm). The sizes at gonad developmental state not connected by the same letter in the Mean SVL Comparisons column are significantly different (all other *P*-values ≤ 0.0181). Data are from specimens collected from 2003 through 2021 in the Greater Everglades Ecosystem, Florida, USA.

Gonad Developmental State	n	Mean SVL Comparisons	Min	10%	25%	Median	75%	90%	Max	Reproductive Status
Undeveloped ♀ & ♂	835	A	42	57	60	67	106	157	283	Non-reproductive
♂ Flaccid Testes	368	B	58	133	165	187	212	232	360	Non-reproductive
♂ Semi-turgid Testes	246	C	125	167	186	205	229	251	347	Reproductive
♂ Turgid Testes	153	D	142	182	194	212	231	265	330	Reproductive
♀ Primary Follicles	384	E	151	178	195	219	260	339	498	Non-reproductive
♀ Secondary Follicles	80	F	184	206	239	276	380	424	478	Reproductive
♀ Oviductal Eggs	56	F	185	216	246	276	307	382	475	Reproductive

Table 2. Estimated size-stage class demarcations (snout-vent length; SVL, cm) and gonad developmental state (Table 1) and mean tail lengths by sex for invasive Burmese pythons (*Python molurus bivittatus*) in southern Florida, USA. Data are from specimens collected from 1995 through 2021 in the Greater Everglades Ecosystem.

Size-stage Class	♀ Body Length (cm SVL)	% ♀ Tail to Total Length	♂ Body Length (cm SVL)	% ♂ Tail to Total Length
Juvenile	39–150.9	12.6	42–124.9	12.5
Sub-adult	151–205.9	12.3	125–181.9	12.8
Adult	206+	11.8	182+	13.1

juvenile males. The smallest 10% of reproductively active females (developing secondary follicles or oviductal eggs) were approximately 206 cm SVL while the smallest 10% of males exhibiting turgid testes were approximately 182 cm SVL, so these thresholds were considered as transitional from sub-adults to adults of each sex (Table 2).

We used individuals with both SVL and complete tail length measurements to calculate the average tail length for each sex across size-stage classes (Table 2). Proportion of tail length to body length did not differ between the size-stage classes but did differ between the sexes ($F_{1,2450} = 204.4130$, $p < 0.0001$) and between the sexes of each size-stage class (juvenile = $F_{1,1207} = 3.9234$, $p = 0.0478$; sub-adults = $F_{1,539} = 67.3810$, $p < 0.0001$; adults = $F_{1,716.6} = 501.2598$, $p < 0.0001$). Further, we provide two expressions (EQ1: $R^2 = 0.90$, $n = 287$ and EQ2: $R^2 = 0.75$, $n = 450$) to approximate tail lengths using an SVL measurement for adults of each sex:

EQ1: Adult female tail length (cm) = 4.478214 + 0.1165135*SVL (cm)

EQ2: Adult male tail length (cm) = 4.5850061 + 0.1287574*SVL (cm)

For all length-size-stage class relationship equations and graphs by sex, see Suppl. material 2). To estimate sizes of only reproductive adults using only total length measurements (or vice versa with only SVL), we developed two expressions (EQ3: $R^2 > 0.99$, $n = 58$ and EQ4: $R^2 > 0.99$, $n = 186$) from the data:

EQ3: Reproductive adult females:

a) SVL (cm) = -4.25341 + 0.8954965*Total Length (cm)
b) Total Length (cm) = 4.4790281 + 1.1165112*SVL (cm)

EQ4: Reproductive adult males:

a) SVL (cm) = -3.287218 + 0.8818756*Total Length (cm)
b) Total Length (cm) = 4.5850061 + 1.1287574*SVL (cm)

Clutch sizes

We confirmed that wild female Burmese pythons in Florida overall have larger clutch sizes with larger body sizes, but that the number of secondary follicles is likely an overestimate of actual clutch sizes. We excluded individuals exhibiting egg retention (n = 5; see Anderson et al. 2022) in these analyses and results. We found a positive correlation in female body size (SVL) to potential clutch size (secondary follicles or oviductal eggs; R^2 = 0.81, n = 115, p < 0.0001; Suppl. material 3) that could be predicted using the following regression equation (EQ5):

EQ5: Potential clutch size = -46.95676 + 0.282554*SVL (cm)

However, potential clutch size was larger when enumerating secondary follicles (mean = 44.5, SE = 2.6641, 95% CI = 39.3–49.9, range = 8–103, n = 70) than oviductal eggs (mean = 30.8, SE = 3.0617, 95% CI = 24.7–36.8, range = 11–72, n = 53; t_{121} = -3.68069, p = 0.0004). The regression equations for each state (EQ6: R^2 = 0.81, n = 65 and EQ7: R^2 = 0.88, n = 51) are as follows:

EQ6: Potential clutch size of secondary follicles only =
-46.46219 + 0.2907525*SVL (cm)

EQ7: Potential clutch size of oviductal eggs only = -35.8948 + 0.2306006*SVL (cm)

In our dataset, eight instances of known females were found associated with nests. We found that female SVL was positively correlated with the total number of oviposited eggs in a clutch, and developed an equation to describe the association (EQ8; R^2 = 0.81, DF = 7, p = 0.0023):

EQ8: Oviposited eggs (actual clutch size) = -31.9255 + 0.2152397*SVL (cm)

The number of oviposited eggs from 13 wild nests (Table 3) were 22–84 (mean = 49, SD = 22), the largest of which was from a nest discovered after hatching without a known maternal female (Nest 8; and therefore could not be associated with female

body sizes above). In 2021, we monitored two nests (Nests 5 & 6) and found that lay dates were both approximately 15 May (±3 d; exact dates unknown due to sampling rate). One of those two nests was destroyed by a nest predator (Nest 5; see Currylow et al. 2022c), but the successful nest was ultimately incubated in the laboratory, commenced hatching approximately 63 d after being laid, and took 3 days to hatch completely (19–21 July, 2021). We found that all the known hatching dates were also in July (Table 3). Of the four nests with notes and hatched eggs (Table 3, Nests 6, 7, & 9), Nest 6 comprised 9 inviable of 40 total, Nest 7 comprised 9 inviable eggs of the 79 eggs total, and Nest 9 comprised 2 inviable of the 39 total. We noted that a small proportion of oviposited eggs in two of the nests were discolored, misshapen, and smaller than the rest in the clutch and proved to be inviable (Nest 6 = 6 of 40; Nest 10 = 1 of 24).

Seasonal trends

We found that there were changes in the size (SVL) of pythons captured across months that confirm annual seasonal patterns in both hatchling and adult Burmese pythons in Florida ($F_{11, 3375} = 164.7925$, $p < 0.0001$). Pythons were captured year-round (see Suppl. material 4), but most annual captures were juveniles between the months of July through October when the YoY emerge (Fig. 4). To see adult python captures separated out by sex across months, see Suppl. material 5.

Hatchling emergence

We confirmed that Burmese pythons synchronously hatch and disperse from nests during a discrete annual time period, but also that the YoY (those emerging before the calendar-year end) can be distinguished from small yearling pythons during this period from summer into the fall months in Florida. Of the nests we discovered dur-

Table 3. Opportunistically recorded parameters of Burmese python (*Python molurus bivittatus*) nests discovered during work in the Greater Everglades Ecosystem, Florida, USA from 2006 through 2022. SVL = Snout-vent length.

	Maternal SVL (cm)	Approx. lay date	Approx. hatch date	# Eggs or shells	Citation
Nest 1	414	5-17-2006	-	46	Snow et al. 2007a
Nest 2	286	-	7-2008	27	Snow et al. 2010
Nest 3	264	-	7-29-2009	22	Wolf et al. 2016
Nest 4	265	5-2015	7-02-2015	25	Hanslowe et al. 2016
Nest 5	396	5-13-2021	NA	64	Currylow et al. 2022c
Nest 6	321	5-18-2021	7-20-2021	40	Current Study
Nest 7	-	-	7-18-2021	79	Current Study
Nest 8	-	-	2020	84 (shells)	Current Study
Nest 9	315	-	7-13-2022	39	Current Study
Nest 10	260	-	7-30-2022	24	Current Study
Nest 11	-	-	-	74 (shells)	Current Study
Nest 12	-	-	-	71 (shells)	Current Study
Nest 13	-	-	-	46 (shells)	Current Study

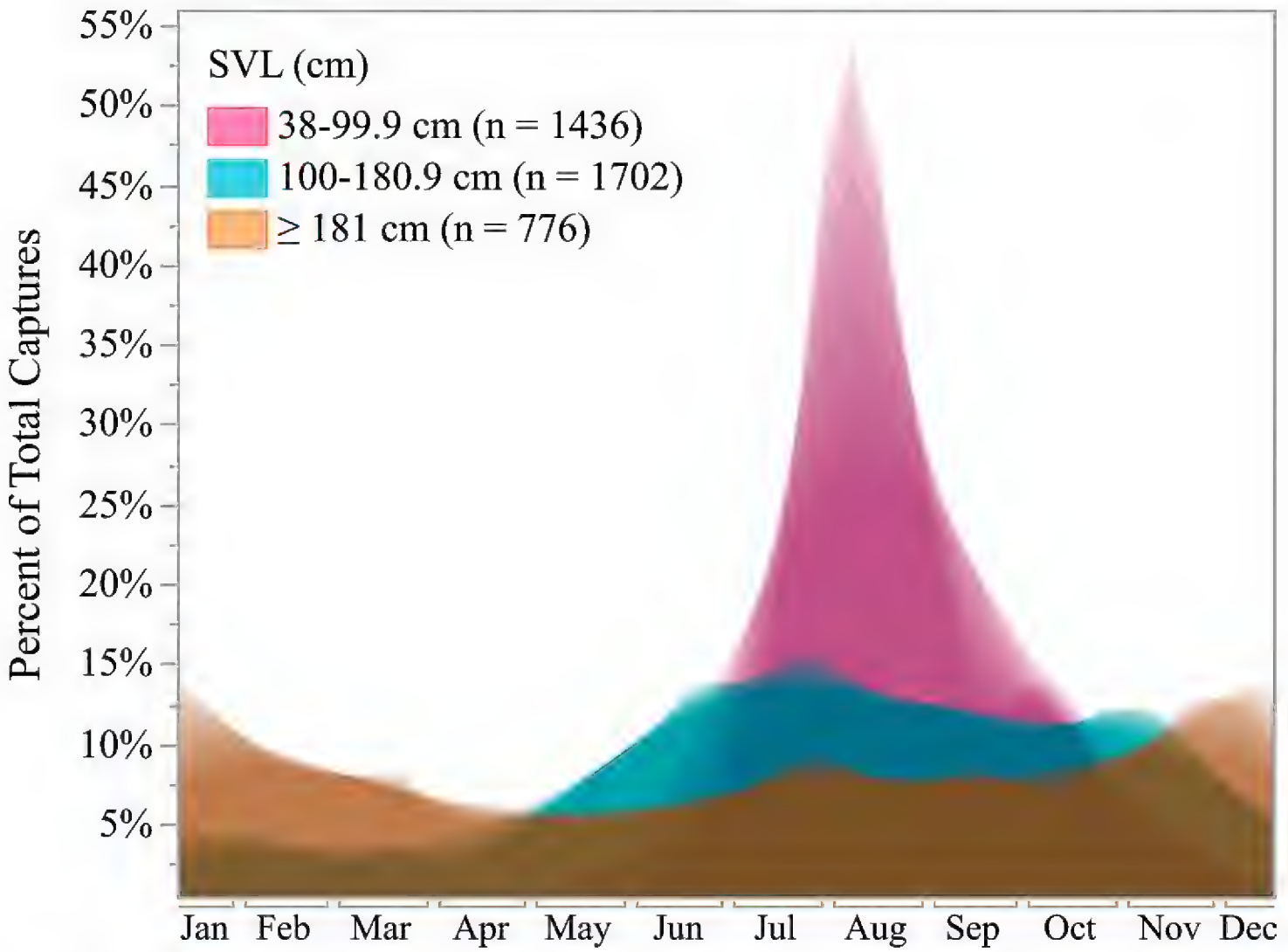

Figure 4. Density histogram of the proportion of 3,908 Burmese pythons (*Python molurus bivittatus*) across months by size bins (in snout-vent length; SVL; in cm) from southern Florida, USA between 1995 and through 2021. Size bins generally correspond to size-stage class but vary between sexes (see text).

ing this work, all with known hatch dates hatched in July (Table 3). Further, when only looking at the juvenile size-stage class in the larger dataset, we found that the YoY captured during July – October (n = 1,486) were distinctly smaller (SVL) than other juvenile pythons on the landscape ($F_{11,1287} = 72.3710$, $p < 0.0001$). During these four months, median sizes for YoY hatchlings were 62.9 cm SVL (interquartile range 58.6–71.5 cm) and 125.0 g (interquartile range = 107.0–194.0 g; see Suppl. material 6). By November, juvenile pythons measured 93.5 cm SVL median (interquartile range 84.0–101.0 cm) at 548 g (interquartile range 360.0–680.0 g) and started to become indistinguishable from juvenile pythons from the previous year (Fig. 5).

Reproductive cycles

We also confirmed that adult Burmese pythons exhibit a regular annual reproductive cycle, but that we could further define reproductive seasonality of breeding, oviposition, incubation, and that not all individuals undergo these changes every year. We found that adult pythons in southern Florida exhibited annual reproductive cycles in the average monthly recrudescence and regressive states of the ovaries ($\chi^2_{33,383} = 290.435$,

$p < 0.0001$) and testes ($\chi^2_{22,535} = 282.567$, $p < 0.0001$; Fig. 6). Of the 210 pythons having either turgid testes or preovulatory secondary follicles, 192 (91%) were found between December and March in both sexes (Fig. 6). We found that females may have primary follicles throughout the year (commonly in addition to secondary follicles or

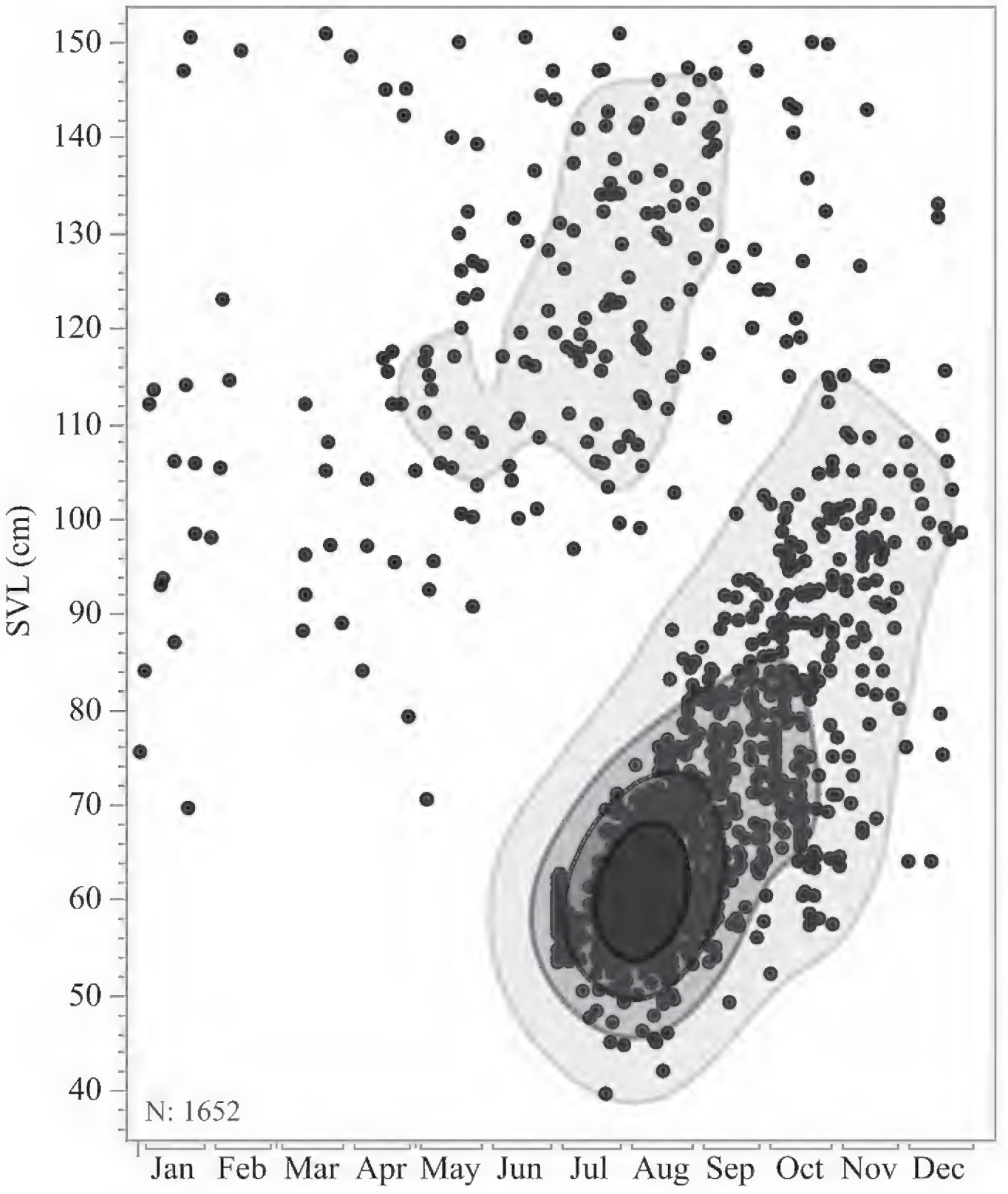

Figure 5. Juvenile Burmese python (*Python molurus bivittatus*) captures (dark dots) across months of the year (scale in Julian days) by snout-vent length (SVL; cm) in southern Florida, USA (1995–2021). Shaded probability polygons represent 25%, 50% ,75%, and 99% data density contours. The separation of the dark lower right set of overlapping polygons from the rest of the points earlier in the year highlights the months of highest juvenile encounters (July through October) and their correlated spread of sizes over those months, helping to distinguish the smaller young-of-year (YoY) hatchlings from other juveniles. Outside the July into October timeframe, YoY and juveniles from the prior year cannot be confidently distinguished.

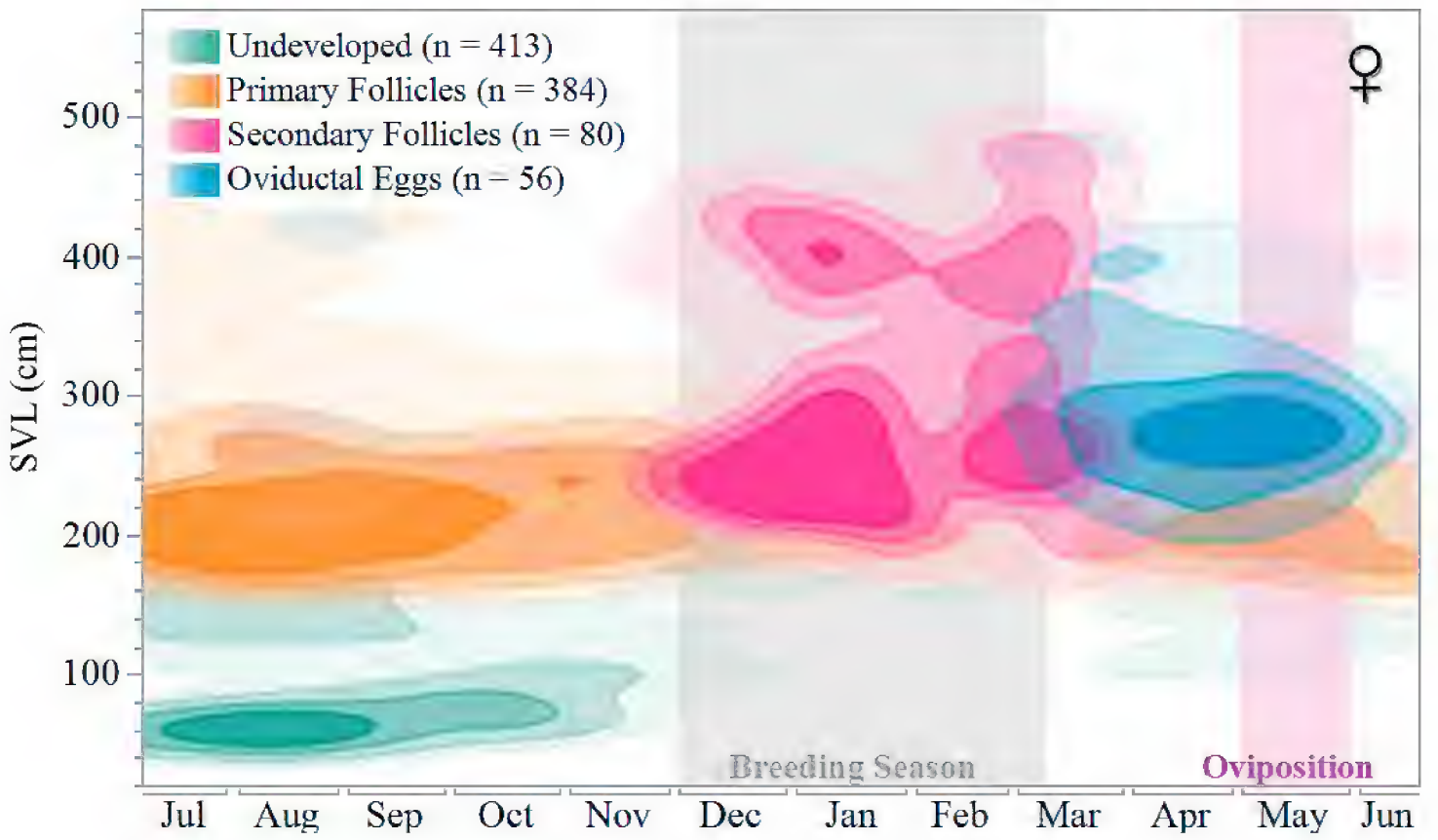

Figure 6. Annual reproductive cycle probability density contour plots of Burmese python (*Python molurus bivittatus*) females (top; *n* = 933 snakes) and males (bottom; *n* = 1,123 snakes) in southern Florida, USA. Python sizes (snout-vent length; SVL, cm) are shown across months of the year (scale in Julian days) and separated by observed gonad developmental state (colored density polygons at 25%, 50% ,75%, and 99% data contours) from necropsied individuals collected from 2003 through 2021. Grey shaded vertical band represents purported breeding season (approximately 100 days December into March) when seasonal gonadal recrudescence peaks (see text). The purple shaded vertical band for females represents hypothesized oviposition timing (e.g., initiation of nesting season) based on presence of oviductal eggs in specimens, field observations, and published accounts. Note: sample sizes are low for gravid females due to low encounter rates during nesting.

oviductal eggs) but exhibited gonadal recrudescence (i.e., vitellogenic/secondary follicles) during that December into March period in 70 of 85 instances. In males, we found individuals to have flaccid testes throughout the year, but we found males exhibited gonadal recrudescence most frequently beginning in November through March (semi-turgid testes in 162 of 189 instances) and turgid testes were found in December and into March (133 of 141 instances) followed by gonadal regression (Fig. 6). Because these time periods during which gonadal recrudescence occurred were correlated in both sexes and with numerous field observations of courtship and breeding (Smith et al. 2015; Smith et al. 2016), we further refine the southern Florida Burmese python breeding season here as lasting approximately 100 days, from early December into mid-March (Fig. 6).

Oviductal eggs were found in females from March through May (52 of 58 instances; Fig. 6). Of the nests we opportunistically encountered during this study (Table 3), all known lay dates were in May (oviposition timing), and all known hatch dates were in July (a two-month incubation period). Due to the presence of eggs in 5 of 58 female pythons outside of those months (e.g., August through December), we determined they had retained oviductal eggs from a prior reproductive season (see Anderson et al. 2022). One of these five females also showed signs of egg resorption in the month of August. Additionally, we recorded gonadal state in 184 adult females during the months of December through May, 67 of which we found to be in gonadal latency (i.e., non-reproductive, having non-developed follicles). Those 67 non-reproductive adult females averaged shorter SVLs (265.3 cm, SE = 8.3501) than the reproductive females (307.7 cm, SE = 6.3735) during this time, but there was no length difference when only looking at animals exceeding the upper 95% of the mean SVL (> 302.5 cm; n = 63) and 24% of those individuals were still not reproductive.

Discussion

The introduction and subsequent spread of invasive species is an enormous management issue that is complex (Vitousek et al. 1996), damaging, and costly (Diagne et al. 2021; Fantle-Lepczyk et al. 2022). Characteristics associated with invasiveness remain elusive (Hayes and Barry 2008) because of complex environment interactions and feedbacks with the invader (Gurevitch et al. 2011), but demographic processes (e.g., survival, growth, reproduction) are fundamental to population structure (Griffith et al. 2016), determining whether invasions proceed or fail. Despite the importance, basic components of reproductive phenology data are limited for many invasives, such as the cryptic Burmese python. In a system like the Greater Everglades Ecosystem which is known for high floral and faunal diversity, including dozens of threatened or endangered faunal species (Brown et al. 2006), knowledge of the biological traits of species can assist with prediction, prevention, and control of invasion (Govindarajulu et al. 2005). Here, we elucidated size distribution, size at maturity, potential clutch sizes, and seasonal trends in emergence and reproductive phenology of the highly invasive Burmese python.

Size distribution

Though there are some limitations (e.g., many of the specimens used in this study were captured while crossing roads or levees and may not be representative of the population as a whole), this is the first time a robust and long-term dataset has been available to describe the seasonal morphometric and reproductive trends of wild Burmese pythons and for the invasive population found in the Greater Everglades Ecosystem, FL, USA. Not all necropsy data were collected from every specimen due to specimen condition, staffing, or data needs, and such incomplete or inconsistent data collection methods can prevent comparisons across studies. Therefore, to facilitate cross-study and future comparisons, we present several equations and reference figures derived from a large sample size to define length relationships (i.e., total, tail, and snout-vent lengths; EQ1–EQ4; Fig. 2; Suppl. material 2).

We found that python size distribution is broader than previously estimated for this invasive population (Reed and Rodda 2009; de Vosjoli and Klingenberg 2012; Krysko et al. 2012) as our smallest hatchlings were under 40 cm SVL and the largest adults reached nearly 500 cm SVL (557 cm total length). In comparison, another dataset on hatchling Burmese python sizes reported a range from 58 to 66 cm SVL (Josimovich and Currylow 2021), though Snow et al. (2007b) reported a hatchling of 38 cm total length, they also stated that it was probably an inaccurate measurement. The average sizes of adult females in our dataset (277 cm SVL, 17,255 g) were 79% longer and nearly 4 times heavier than the average for males (155 cm SVL, 4,394 g). Only one python out of the longest 90 measurements in our dataset (those > 370 cm SVL; 409–557 cm total length; 17,950–84,800 g) was male (400 cm SVL and 44,000 g; no tail or total length was recorded). In comparison, the largest Burmese pythons from their native range have been reported to reach 579–610 cm total length (Wall 1921; Murphy and Henderson 1997; Snow et al. 2007b). Record-breaking female Burmese pythons from across southern Florida appear to incrementally increase the recorded maximum size each year according to media reports, but the largest male on record remains unmatched at 438 cm SVL (493 cm total length, 63,500 g; Easterling and Bartoszek 2019).

Size at maturity

As we hypothesized, our data support the sexual size dimorphism expected in size at maturity as summarized by Reed and Rodda (2009), though, our estimates appear to be somewhat smaller. Additionally, we are aware of only two confirmed accounts of size at maturity described in the literature, both in females (Wall 1921; Willson et al. 2014). We found that minimally-sized mature individuals are slightly shorter than previous estimates for males (ca. 208 cm total length vs. 210 cm reported by de Vosjoli and Klingenberg 2012 but see Reed and Rodda 2009) and for females (ca. 229 cm total length vs. 259 cm total length reported by Pope 1961). There are no other known records of verified minimum size at maturity in wild male Burmese pythons with the closest relative, the Indian python (*P. m. molurus*), only very recently reported from the native range to be 172 cm SVL (198 total length; Vishnu et al. 2021). Likewise

in females, a single prior report noted that the smallest reproductive female Burmese python known was found in May 2013 from the southern Florida population and reached only 210 cm total length with 11 oviductal eggs (Willson et al. 2014), and, very recently, another female of this size was reported to be gravid from the same population (Anderson et al. 2022).

While investigating size at maturity, we also found that there were differences in the proportion of tail length to body length between the sexes in every size-stage class. However, the relatively small difference (0.1%) was barely statistically significant in the juvenile size-stage class when reproductive organs are not yet developed, and the result is likely not biologically meaningful. Subadult differences grew somewhat, but only adult python tail proportions were consistently different in a functional way (i.e., hemipene storage). Adult female tails were shorter, averaging 11.8% of their total lengths compared to males whose tails were, on average, 13.1% of their total length. This proportion and the equations derived from the data (EQ1–EQ4) can aid in the evaluation of data from differing research reports that were previously incomparable due to inconsistent collection methods or measurements. For example, applying our proportion estimates and equations to the largest male in our dataset with only SVL recorded (400 cm SVL), we can estimate that his total length was approximately 452–456 cm. Further, using these equations, probable length can be estimated for individual specimens with damaged (i.e., incomplete) tails that would have otherwise rendered total length measurements indeterminable.

Clutch sizes

A critical factor in understanding population growth potential is the lifetime egg production and survival of females. To parameterize such models, researchers need to start with estimates of annual reproductive potential. We hypothesized that python potential clutch size would correlate with maternal body size, and we found the relationship could be estimated using maternal body size (in cm SVL; see EQ5). Though limited in sample size, we were able to show that true clutch size (oviposited eggs) also increased with maternal body size (in SVL; Table 3). However, we further found that a count of secondary follicles (often used to estimate clutch size at the time of python removal) is likely to overestimate actual clutch sizes (e.g., EQ6 vs EQ7). Reports of necropsied Burmese pythons containing unusually high "egg" counts and inferred as directly removing a high number of pythons from the population warrant cautious interpretation. There are little data on nest success and hatchling survival, adult females may not ovulate all follicles, ovulated follicles may not be otherwise viable (e.g., lack appropriate yolk provisions or not fertilized), follicles or oviductal eggs may be resorbed, or expelled within a clutch at a visible size difference. For example, one adult female python (482 SVL, 74,600 g) from Everglades National Park in 2012 was found to contain 87 oviductal eggs with 2 that appeared to be in the process of being resorbed (Krysko et al. 2012). Similarly, the nests we discovered as part of this study were noted to contain several inviable and misshapen eggs, with some being visibly smaller (though few

were enumerated at the time). The prevalence of these "slugs" is unknown in the wild population but are commonly referenced in the herpetoculture literature (Blackburn 1998). Though some reports include "inviable" eggs as a subset of total clutch sizes, it is not known if smaller inviable eggs are considered in the same way, if most clutches contain them, or if those reports that do not explicitly include inviable counts simply lump them all together, possibly skewing clutch size estimates. There also is evidence that females fail to oviposit their entire clutch, retaining some shelled oviductal eggs beyond normal oviposition timing (Anderson et al. 2022), however the prevalence and implications of this are still unclear.

We found that clutch sizes including only oviductal eggs or laid eggs ranged from 11 to 84 (mean = 34, SD = 18, median = 27, interquartile range = 24–46, n = 66). This range is in line with previously reported clutch sizes from this population (21, 27, 29, 35, 37, 46, 79, 85, and 87; Snow et al. 2007a, b; Krysko et al. 2008; Snow et al. 2010; Krysko et al. 2012), which all fall within those thought to be typical clutch sizes from their native range as reported by Wall (1921). Yet, our three highest counts of potential clutch size (those above the highest reported number of oviductal eggs of 87 from southern Florida; Krysko et al. 2012) were all pre-ovulatory follicles numbering 89, 90, and 103 from females found in Feb 2020 (SVL = 475 cm), Dec 2020 (SVL = 430 cm), and Jan 2017 (SVL = 429 cm), respectively. Similarly high numbers of preovulatory follicles have been reported (Rochford et al. 2010), whereas the highest number of oviductal eggs we documented was 72 from a 475 cm SVL female found in Mar 2019. These numbers are somewhat higher than those reported in a short note by Brien et al. (2007) (mean = 36, n = 8, range = 19–46), but those authors did not distinguish the potential clutch sizes between secondary (pre-ovulatory vitellogenic) follicles and oviductal eggs.

Seasonal trends

Hatchlings

The data supported our hypothesis that pythons synchronously hatch and disperse from nests, appearing on the Florida landscape in large numbers during the summer and fall months (July into October) and peaking in August (Fig. 4). This size-stage class constitutes the highest number of captures throughout the year, and the initial surge in July corresponds well with hatch date observations (Table 3). However, from this long-term dataset, we were further able to distinguish the YoY hatchlings from those smaller individuals remaining on the landscape from a prior year during a period between July and October (Fig. 5). This distinction helps us understand variation in size over the first year of life, a parameter vital to life tables used to estimate population growth trends. During the summer months, we can relatively accurately identify a YoY hatchling based on SVL and month of capture. However, more work needs to be done to determine whether estimates can be generated for size-stage classes (i.e., size relative to length of time in days or years), such as radio-tracking wild Burmese pythons long-term from hatching.

Reproductive cycles

A clear understanding of reproductive timing can not only inform population models but also aid managers in targeting times of year when control mechanisms may be most effective in arresting population growth. In this study, we confirmed our hypothesis that adult Burmese pythons exhibit annual reproduction and further refined the biologically significant time periods (i.e., breeding season, oviposition timing, and incubation period). We found that seasonal recrudescence of gonadal structures aligns well with field observations of gregarious behaviors (e.g., Smith et al. 2015; Smith et al. 2016). Using this paired timing among gonadal recrudescence and regression along with the presence or absence of breeding behaviors, we discretely defined the Burmese python breeding season in southern Florida as the approximately 100 days beginning in December and ending mid-March (see Fig. 6). In northern India at a similar latitude but much higher elevation than southern Florida, reports of the closely related *P. m. molurus* exhibit heightened breeding activity during February and March, but may extend into August (Bhupathy and Vijayan 1989). However, more aligned with observations in southern Florida, there is evidence indicating that pythons breed in Sri Lanka December through February (Wall 1921), and *P. m. bivittatus* breed in Thailand December to mid-March (Smith et al. 2021).

Breeding season may be the time that adult male Burmese pythons in southern Florida become most vagile annually. Though we cannot account for effort in our dataset, most adult males are captured between the months of November through March, presumably because they are in search of mates. While adult female captures remain relatively steady across months at 2–5% of all captures, adult male captures increase to 7%, 10%, and 12% of total numbers in November through January, decreasing to 6% and 5% in February and March, and then remain under 4% for the remainder of the year (see Suppl. materials 4, 5). Snow et al. (2007b) also reported multiple captures during November through January, 35% of which were from December through January alone, suggesting that the uptick coincides with seasonal behaviors such as breeding.

We found that 87% of reproductive-sized females physiologically prepare for nesting by beginning vitellogenesis (developing secondary follicles) in November and continuing into March (Fig. 6, top). Females are ovigerous (having oviductal eggs) from March into May. This is a shorter period than the Krysko et al. (2008) estimate of January through April but comparable to Snow et al. (2010). We also saw that female pythons oviposit, starting in May (Fig. 6, top). This is concordant with radio-tracked females in Thailand that have been observed to nest between April and June (Smith et al. 2021). However, not all adult females in our dataset were reproductive during these periods. We found that approximately 36% (n = 67) of adult females (n = 184) were non-reproductive (having undeveloped follicles) during the months of December through May (Fig. 6, top). This indicates that approximately a third of all females in any given year may not reproduce, perhaps reproducing every 2–3 years. Literature supports a biennial reproductive cycle in these and other snakes and could be due to lowered body condition and recovery following nesting (Bertona and Chiaraviglio

2003; Reed and Rodda 2009; Willson et al. 2011). Burmese pythons exert effort as they exhibit nest guarding/defense (e.g., Currylow et al. 2022c) and incubate eggs through shivering thermogenesis during brooding (Benedict 1932; Hutchison et al. 1966; Van Mierop and Barnard 1978; Snow et al. 2010).

Our limited dataset on incubation/prehatching period (e.g., Table 3) indicates an approximately two-month development period, which agrees with the current literature estimates and is suggested to be somewhat regulated by temperatures (Pope 1961; Van Mierop and Barnard 1976). There is a paucity of precise data on oviposition timing for wild pythons in southern Florida (Harvey et al. 2008), but radio-tracked females have led to the narrowest windows thus far. We found the two females we tracked in 2021 oviposited very close in time (within 6 days in mid-May; Table 3, Nests 5 & 6). The nests that had hatch date recorded (Table 3, Nests 3, 4, 6, 7, 9 & 10) did so in July, often within days of each other. The nest we monitored throughout 2021 (Nest 6) took about 63 days to incubate and 3 days to complete hatching. This is concordant with the captive literature where oviposition usually happens approximately two months after breeding, incubation lasts anywhere from 53 to 88 days, and hatching is complete after a couple days (Ross and Marzec 1990; Murphy and Henderson 1997).

Management implications

Management of Burmese pythons in Florida is costly due to difficulties associated with low detection and the vast wilderness of the Greater Everglades Ecosystem. Our findings regarding python size distribution and reproductive phenology provide standardized equations for direct cross-study comparisons that can inform population models and help managers target pythons for removal with a greater return on investment. For example, we have determined the size threshold for adult males, which provides managers operating scout snake programs (i.e., Fitzgerald et al. 2021) a reliable metric to easily assess adult males as future scout snakes. Additionally, our data indicate that male Burmese pythons are primarily seeking mates for 100 days from December through March, so that will likely be the most effective window of time for managers to physically visit their scout snakes and survey for associate snakes. When deciding where to direct limited management resources, managers can consider targeting specific size-stage classes by time of year because we defined the above-listed breeding season and found that pythons hatch synchronously and disperse on the landscape from July through October. And because we found that adult females oviposit in May and attend their nests during the subsequent two-month incubation period, that timeframe could be targeted for removal of those individuals with the highest reproductive potential along with their entire clutch of eggs (e.g., using dogs trained to detect pythons). Our finding that secondary follicles do not necessarily represent clutch size can help managers understand the number of total potential pythons removed with each individual reproductive female. Yet we did find that true clutch size increased with female body size, so the removal of fewer but larger females could be considered by managers to be a

higher priority over removing sheer numbers of total pythons. We found that YoY can be distinguished from the older juveniles during a July into October annual window, which can afford managers the relative number of hatchlings that naturally survive into a second year in their management unit. As research and management activities continue in concert, detection and control will become more effective with studies that refine our understanding of python demographics, reproduction, and seasonal trends.

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References

Aldridge RD (1979) Female reproductive cycles of the snakes *Arizona elegans* and *Crotalus viridis*. Herpetologica 35: 256–261. https://www.jstor.org/stable/3891696

Anderson GE, Ridgley FN, Josimovich JM, Reed RN, Falk B, Yackel Adams AA, Currylow AF (2022) Egg retention in wild-caught *Python bivittatus* in the Greater Everglades Ecosystem, Florida, USA. The Herpetological Journal 32(3): 109–113. https://doi.org/10.33256/32.3.109113

Benedict FG (1932) The physiology of large reptiles: with special reference to the heat production of snakes, tortoises, lizards and alligators. Carnegie Institution of Washington, Washington, 539.

Bertona M, Chiaraviglio M (2003) Reproductive biology, mating aggregations, and sexual dimorphism of the Argentine boa constrictor (*Boa constrictor occidentalis*). Journal of Herpetology 37(3): 510–516. https://doi.org/10.1670/122-02A

Bhupathy S, Vijayan VS (1989) Status, distribution, and general ecology of the Indian python, *Python molurus molurus*. Linn. in Keoladeo National Park, Bharatpur, Rajasthan, India. Journal of the Bombay Natural History Society 86: 381–387.

Blackburn DG (1998) Resorption of oviductal eggs and embryos in squamate reptiles. The Herpetological Journal 8: 65–71.

Brien ML, Cherkiss MS, Johnson VM, Mazzotti FJ, Snow RW (2007) *Python molurus bivittatus* (Burmese Python). Clutch size. Herpetological Review 38: 242–243.

Brown MT, Cohen MJ, Bardi E, Ingwersen WW (2006) Species diversity in the Florida Everglades, USA: A systems approach to calculating biodiversity. Aquatic Sciences 68(3): 254–277. https://doi.org/10.1007/s00027-006-0854-1

Burger J, Zappalorti RT, Gochfeld M (1987) Developmental effects of incubation temperature on hatchling pine snakes *Pituophis melanoleucus*. Comparative Biochemistry and Physiology. A. Comparative Physiology 87(3): 727–732. https://doi.org/10.1016/0300-9629(87)90390-2

Burkett-Cadena ND, Blosser EM, Loggins AA, Valente MC, Long MT, Campbell LP, Reeves LE, Bargielowski I, McCleery RA (2021) Invasive Burmese pythons alter host use and virus infection in the vector of a zoonotic virus. Communications Biology 4(1): 804. https://doi.org/10.1038/s42003-021-02347-z

Card DC, Perry BW, Adams RH, Schield DR, Young AS, Andrew AL, Jezkova T, Pasquesi GIM, Hales NR, Walsh MR, Rochford MR, Mazzotti FJ, Hart KM, Hunter ME, Castoe TA (2018) Novel ecological and climatic conditions drive rapid adaptation in invasive Florida Burmese pythons. Molecular Ecology 27(23): 4744–4757. https://doi.org/10.1111/mec.14885

Currylow AF, Hanley BJ, Holcomb KL, Shields T, Boland S, Boarman WI, Vaughn M (2022a) A decision tool to identify population management strategies for common ravens and other avian predators. Human-Wildlife Interactions 15(3): Article 25. https://doi.org/10.26077/e056-1a58

Currylow AF, Falk BG, Yackel Adams AA, Romagosa C, Josimovich JM, Rochford M, Cherkiss M, Nafus MG, Hart K, Mazzotti F, Snow R, Reed RN (2022b) Size distribution and reproductive data of the invasive Burmese python (*Python molurus bivittatus*) in the Greater Everglades Ecosystem, Florida, USA, 1995–2021: U.S. Geological Survey data release. https://doi.org/10.5066/P9CZI2KO

Currylow AF, McCollister MF, Anderson GE, Josimovich JM, Fitzgerald AL, Romagosa CM, Yackel Adams AA (2022c) Face-off: Novel depredation and nest defense behaviors between an invasive and a native predator in the Greater Everglades Ecosystem, Florida, USA. Ecology and Evolution 12(2): e8639. https://doi.org/10.1002/ece3.8639

de Vosjoli P, Klingenberg R (2012) Burmese pythons: Plus reticulated pythons and related species. Fox Chapel Publishing, USA.

Diagne C, Leroy B, Vaissière A-C, Gozlan RE, Roiz D, Jarić I, Salles J-M, Bradshaw CJA, Courchamp F (2021) High and rising economic costs of biological invasions worldwide. Nature 592(7855): 571–576. https://doi.org/10.1038/s41586-021-03405-6

Dorcas ME, Willson JD, Reed RN, Snow RW, Rochford MR, Miller MA, Meshaka Jr WE, Andreadis PT, Mazzotti FJ, Romagosa CM, Hart KM (2012) Severe mammal declines coincide with proliferation of invasive Burmese pythons in Everglades National Park. Proceedings of the National Academy of Sciences of the United States of America 109(7): 2418–2422. https://doi.org/10.1073/pnas.1115226109

Easterling I, Bartoszek I (2019) *Python bivittatus* (Burmese python). Maximum male size. Herpetological Review 50: 399–400.

Emery J-P, Mitchell NJ, Cogger H, Agius J, Andrew P, Arnall S, Detto T, Driscoll DA, Flakus S, Green P, Harlow P, McFadden M, Pink C, Retallick K, Rose K, Sleeth M, Tiernan B, Valentine LE, Woinarski JZ (2021) The lost lizards of Christmas Island: A retrospective assessment of factors driving the collapse of a native reptile community. Conservation Science and Practice 3(2): e358. https://doi.org/10.1111/csp2.358

Falk BG, Snow RW, Reed RN (2016) Prospects and limitations of citizen science in invasive species management: A case study with Burmese pythons in Everglades National Park. Southeastern Naturalist 15(sp8): 89–102. https://doi.org/10.1656/058.015.sp806

Fantle-Lepczyk JE, Haubrock PJ, Kramer AM, Cuthbert RN, Turbelin AJ, Crystal-Ornelas R, Diagne C, Courchamp F (2022) Economic costs of biological invasions in the United States. The Science of the Total Environment 806: 151318. https://doi.org/10.1016/j.scitotenv.2021.151318

Feldman A, Meiri S (2012) Length–mass allometry in snakes. Biological Journal of the Linnean Society. Linnean Society of London 108(1): 161–172. https://doi.org/10.1111/j.1095-8312.2012.02001.x

Fitch HS (1960) Criteria for determining sex and breeding maturity in snakes. Herpetologica 16: 49–51.

Fitzgerald A, Josimovich J, Robinson CJ, Reed R, Currylow AF (2021) Identifying negative sentiment polarity in the Judas Technique. Conservation Science and Practice 3(11): e532. https://doi.org/10.1111/csp2.532

Govindarajulu P, Altwegg R, Anholt BR (2005) Matrix model investigation of invasive species control: Bullfrogs on Vancouver Isand. Ecological Applications 15(6): 2161–2170. https://doi.org/10.1890/05-0486

Griffith AB, Salguero-Gómez R, Merow C, McMahon S (2016) Demography beyond the population. Journal of Ecology 104(2): 271–280. https://doi.org/10.1111/1365-2745.12547

Gurevitch J, Fox GA, Wardle GM, Inderjit, Taub D (2011) Emergent insights from the synthesis of conceptual frameworks for biological invasions. Ecology Letters 14(4): 407–418. https://doi.org/10.1111/j.1461-0248.2011.01594.x

Hanley B, Connelly P, Dennis B (2019a) Another look at the eigenvalues of a population matrix model. PeerJ 7: e8018. https://doi.org/10.7717/peerj.8018

Hanley BJ, Dhondt AA, Dennis B, Schuler KL (2019b) Using time series data to assess recent population dynamics of bald eagles in the northeast United States. Ecosphere 10(11): e02963. https://doi.org/10.1002/ecs2.2963

Hanslowe EB, Falk BG, Collier MA, Josimovich JM, Rahill TA, Reed RN (2016) First record of invasive Burmese python oviposition and brooding inside an anthropogenic structure. Southeastern Naturalist 15(sp8): 103–107. https://doi.org/10.1656/058.015.sp809

Harvey RG, Brien ML, Cherkiss MS, Dorcas M, Rochford M, Snow RW, Mazzotti FJ (2008) Burmese pythons in South Florida: Scientific support for invasive species management; WEC-242; Univeristy of Florida, IFAS Extension, 10. https://doi.org/10.32473/edis-uw286-2008

Hayes KR, Barry SC (2008) Are there any consistent predictors of invasion success? Biological Invasions 10(4): 483–506. https://doi.org/10.1007/s10530-007-9146-5

Hoyer IJ, Blosser EM, Acevedo C, Thompson AC, Reeves LE, Burkett-Cadena ND (2017) Mammal decline, linked to invasive Burmese python, shifts host use of vector mosquito towards reservoir hosts of a zoonotic disease. Biology Letters 13(10): 20170353. https://doi.org/10.1098/rsbl.2017.0353

Hunter ME, Oyler-McCance SJ, Dorazio RM, Fike JA, Smith BJ, Hunter CT, Reed RN, Hart KM (2015) Environmental DNA (eDNA) sampling improves occurrence and detection estimates of invasive Burmese pythons. PLoS ONE 10(4): e0121655. https://doi.org/10.1371/journal.pone.0121655

Hutchison VH, Dowling HG, Vinegar A (1966) Thermoregulation in a brooding female Indian python, *Python molurus bivittatus*. Science 151(3711): 694–696. https://doi.org/10.1126/science.151.3711.694

Josimovich JM, Currylow AF (2021) Hatchling growth experiment dataset from invasive Burmese pythons captured in 2015 in southern Florida: U.S. Geological Survey data release. https://doi.org/10.5066/P9WHSSJ6 [accessed April 2, 2022]

Josimovich JM, Falk BG, Grajal-Puche A, Hanslowe EB, Bartoszek IA, Reed RN, Currylow AF (2021) Clutch may predict growth of hatchling Burmese pythons better than food availability or sex. Biology Open 10(11): bio058739. https://doi.org/10.1242/bio.058739

Krysko K, Nifong J, Mazzotti F, Snow R, Enge K (2008) Reproduction of the Burmese python (*Python molurus bivittatus*) in southern Florida. Applied Herpetology 5(1): 93–95. https://doi.org/10.1163/157075408783489185

Krysko KL, Hart KM, Smith BJ, Selby TH, Cherkiss MS, Coutu NT, Reichart RM, Nuñez LP, Mazzotti FJ, Snow RW (2012) Record length, mass, and clutch size in the nonindigenous Burmese python, *Python bivittatus* Kuhl 1820 (Squamata: Pythonidae), in Florida. Reptiles & Amphibians : Conservation and Natural History 19(4): 267–270. https://doi.org/10.17161/randa.v19i4.13923

Lodge TE (2017) The Everglades handbook: understanding the ecosystem. CRC Press, Taylor & Francis Group, Boca Raton, 440.

McCleery RA, Sovie A, Reed RN, Cunningham MW, Hunter ME, Hart KM (2015) Marsh rabbit mortalities tie pythons to the precipitous decline of mammals in the Everglades. Proceedings. Biological Sciences 282(1805): 20150120. https://doi.org/10.1098/rspb.2015.0120

Miller MA, Kinsella JM, Snow RW, Hayes MM, Falk BG, Reed RN, Mazzotti FJ, Guyer C, Romagosa CM (2018) Parasite spillover: Indirect effects of invasive Burmese pythons. Ecology and Evolution 8(2): 830–840. https://doi.org/10.1002/ece3.3557

Murphy JC, Henderson RW (1997) Tales of giant snakes: A historical natural history of anacondas and pythons. Krieger Publishing Company, Malabar, Florida, 221.

Nafus MG, Mazzotti FJ, Reed RN (2020) Estimating detection probability for Burmese pythons with few detections and zero recaptures. Journal of Herpetology 54(1): 24–30. https://doi.org/10.1670/18-154

Parker MR, Currylow AF, Tillman E, Robinson C, Josimovich J, Bukovich I, Nazarian L, Nafus M, Kluever B, Yackel Adams AA (2021) Using enclosed Y-mazes to assess chemosensory behavior in reptiles. Journal of Visualized Experiments 170: e61858. https://doi.org/10.3791/61858

Pope CH (1961) The giant snakes: the natural history of the boa constrictor, the anaconda, and the largest pythons. Alfred A. Knopf, Inc., New York, 263 pp.

Reed RN, Rodda GH (2009) Giant constrictors: Biological and management profiles and an establishment risk assessment for nine large species of pythons, anacondas, and the boa constrictor; 2009–1202, 302 pp. https://doi.org/10.3133/ofr20091202

Reed RN, Hart KM, Rodda GH, Mazzotti FJ, Snow RW, Cherkiss M, Rozar R, Goetz S (2011) A field test of attractant traps for invasive Burmese pythons (*Python molurus bivittatus*) in southern Florida. Wildlife Research 38(2): 114–121. https://doi.org/10.1071/WR10202

Reed RN, Todd BD, Miano OJ, Canfield M, Fisher RN, McMartin L (2016) Ecology and control of an introduced population of southern watersnakes (*Nerodia fasciata*) in southern California. Herpetologica 72(2): 130–136. https://doi.org/10.1655/HERPETOLOGICA-D-14-00061

Reichert BE, Sovie AR, Udell BJ, Hart KM, Borkhataria RR, Bonneau M, Reed R, McCleery R (2017) Urbanization may limit impacts of an invasive predator on native mammal diversity. Diversity & Distributions 23(4): 355–367. https://doi.org/10.1111/ddi.12531

Rochford MR, Brien ML, Carrigan J, Snow RW, Mazzotti FJ (2010) *Python molurus bivittatus* (Burmese python). Clutch size. Herpetological Review 41: 97.

Rodda GH, Fritts TH (1992) The impact of the introduction of the Colubrid snake *Boiga irregularis* on Guam's lizards. Journal of Herpetology 26(2): 166–174. https://doi.org/10.2307/1564858

Rogers HS, Buhle ER, HilleRisLambers J, Fricke EC, Miller RH, Tewksbury JJ (2017) Effects of an invasive predator cascade to plants via mutualism disruption. Nature Communications 8(1): 14557. https://doi.org/10.1038/ncomms14557

Ross RA, Marzec G (1990) The reproductive husbandry of pythons and boas. Institute for Herpetological Research, 270 pp.

SAS Institute Inc (2021) JMP 16.0.0, SAS Institute Inc., Cary, North Carolina, USA.

Savidge JA (1987) Extinction of an island forest avifauna by an introduced snake. Ecology 68(3): 660–668. https://doi.org/10.2307/1938471

Seigel RA, Collins JT, Novak SS (2001) Snakes: ecology and evolutionary biology. The Blackburn Press, Caldwell, New Jersey, 529 pp.

Shine R, Olsson MM, Moore IT, LeMaster MP, Mason RT (1999) Why do male snakes have longer tails than females? Proceedings. Biological Sciences 266(1434): 2147–2151. https://doi.org/10.1098/rspb.1999.0901

Smith BJ, Rochford MR, Matt B, Cherkiss MS, Mazzotti F, Skip S, Hart KM (2015) Largest breeding aggregation of Burmese pythons and implication for potential development of a control tool. IRCF Reptiles & Amphibians 22: 16–19. https://doi.org/10.17161/randa.v22i1.14025

Smith BJ, Cherkiss MS, Hart KM, Rochford MR, Selby TH, Snow RW, Mazzotti FJ (2016) Betrayal: Radio-tagged Burmese pythons reveal locations of conspecifics in Everglades National Park. Biological Invasions 18(11): 3239–3250. https://doi.org/10.1007/s10530-016-1211-5

Smith SN, Jones MD, Marshall BM, Waengsothorn S, Gale GA, Strine CT (2021) Native Burmese pythons exhibit site fidelity and preference for aquatic habitats in an agricultural mosaic. Scientific Reports 11(1): 7014. https://doi.org/10.1038/s41598-021-86640-1

Snow R, Johnson V, Brien M, Cherkiss M, Mazzotti F (2007a) *Python molurus bivittatus*: Nesting. Herpetological Review 38: 93.

Snow R, Krysko K, Enge K, Oberhofer L, Ludwicka-Bradley A, Wilkins L (2007b) Introduced populations of *Boa constrictor* (Boidae) and *Python molurus bivittatus* (Pythonidae) in southern Florida. In: Henderson RW, Powell R (Eds) Biology of the Boas and Pythons, Eagle Mountain Publishing, Eagle Mountain, Utah, 418–438.

Snow RW, Wolf AJ, Greeves BW, Cherkiss MS, Hill R, Mazzotti FJ (2010) Thermoregulation by a brooding Burmese python (*Python molurus bivittatus*) in Florida. Southeastern Naturalist 9(2): 403–405. https://doi.org/10.1656/058.009.0215

Taillie PJ, Hart KM, Sovie AR, McCleery RA (2021) Native mammals lack resilience to invasive generalist predator. Biological Conservation 261: 109290. https://doi.org/10.1016/j.biocon.2021.109290

Van Mierop LHS, Barnard SM (1976) Observations on the reproduction of *Python molurus bivittatus* (Reptilia, Serpentes, Boidae). Journal of Herpetology 10(4): 333–340. https://doi.org/10.2307/1563071

Van Mierop LHS, Barnard SM (1978) Further observations on thermoregulation in the brooding female *Python molurus bivittatus* (Serpentes: Boidae). Copeia 1978(4): 615–621. https://doi.org/10.2307/1443687

Vishnu SN, Ramesh C, Thirumurugan V, Sathish C (2021) Size matters: First record of minimum male size at maturity and mating of free-ranging, endangered Indian Python *Python molurus*. Asian Journal of Conservation Biology 10: 153–158. https://doi.org/10.53562/ajcb.AQOE1932

Vitousek PM, D'Antonio CM, Loope LL, Westbrooks R (1996) Biological invasions as global environmental change. American Scientist 84: 468–478.

Wall F (1921) Ophidia taprobanica: or, the snakes of Ceylon. HR Cottle, Government printer, Ceylon. https://doi.org/10.5962/bhl.title.53694

Wiles G (1987) Current research and future management of Marianas fruit bats (Chiroptera: Pteropodidae) on Guam. Australian Mammalogy 10: 93–95.

Willson JD, Dorcas ME, Snow RW (2011) Identifying plausible scenarios for the establishment of invasive Burmese pythons (*Python molurus*) in Southern Florida. Biological Invasions 13(7): 1493–1504. https://doi.org/10.1007/s10530-010-9908-3

Willson JD, Snow RW, Reed RN, Dorcas ME (2014) *Python molurus bivittatus* (Burmese python). Minimum size at maturity. Herpetological Review 45: 343–344.

Wolf AJ, Walters TM, Rochford MR, Snow RW, Mazzotti FJ (2016) Incubation temperature and sex ratio of a *Python bivittatus* (Burmese python) clutch hatched in Everglades National Park, Florida. Southeastern Naturalist 15(sp8): 35–39. https://doi.org/10.1656/058.015.sp803

Supplementary material 1

Total Burmese python (*Python molurus bivittatus*)
Authors: Andrea F. Currylow
Data type: figure
Explanation note: Total Burmese python (*Python molurus bivittatus*) records (n = 4,348) per year in this study by size-stage classes (see Currylow et al manuscript text) and sex from the Greater Everglades Ecosystem, Florida, USA. Total numbers of each sex are listed across the top of the graph section. Size-stage classes are distinguishable by color (adult = burnt orange; sub-adult = purple; juvenile = green) and enumerated in the larger bars.
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Link: https://doi.org/10.3897/neobiota.78.93788.suppl1

Supplementary material 2

Relationship of snout-vent lengths (SVLs) and tail lengths to total lengths
Authors: Andrea F. Currylow
Data type: figure
Explanation note: Relationship of snout-vent lengths (SVLs) and tail lengths to total lengths (all in cm) for all intact male and female Burmese pythons (*Python molurus bivittatus*) captured 2004–2021 from the Greater Everglades Ecosystem, Florida, USA. Size-stage classes are distinguished by color (adult = burnt orange; sub-adult = purple; juvenile = green) and individual characteristic equations are displayed for each cross variable in the upper left of each graph. Sample sizes for size-age class are listed in the center bottom of each sex group.
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Link: https://doi.org/10.3897/neobiota.78.93788.suppl2

Supplementary material 3

The potential clutch sizes

Authors: Andrea F. Currylow

Data type: figure

Explanation note: The potential clutch sizes using the number of secondary follicles (pink) or number of oviductal eggs (blue) by snout-vent lengths (SVL in cm) of Burmese pythons (*Python molurus bivittatus*). The shaded areas around the fit lines are 95% confidence of fit buffers. Data were collected from animals across the Greater Everglades Ecosystem, Florida, USA from 2004–2021.

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Link: https://doi.org/10.3897/neobiota.78.93788.suppl3

Supplementary material 4

Percent of total Burmese python (*Python molurus bivittatus*)

Authors: Andrea F. Currylow

Data type: figure

Explanation note: Percent of total Burmese python (*Python molurus bivittatus*) captures from southern Florida, USA each month of all years (1995–2021) combined by sex. Total numbers are displayed in the legend and individual month totals by sex are displayed above each bar within that month.

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Link: https://doi.org/10.3897/neobiota.78.93788.suppl4

Supplementary material 5

Total number of adult Burmese python (*Python molurus bivittatus*)
Authors: Andrea F. Currylow
Data type: figure
Explanation note: Total number of adult Burmese python (*Python molurus bivittatus*) captures across months for all recorded years (2001–2021) separated by sex (red = females, blue = males). Data were collected from animals across the Greater Everglades Ecosystem, Florida, USA.
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Link: https://doi.org/10.3897/neobiota.78.93788.suppl5

Supplementary material 6

Juvenile Burmese python (*Python molurus bivittatus*)
Authors: Andrea F. Currylow
Data type: figure
Explanation note: Juvenile Burmese python (*Python molurus bivittatus*) morphometric data (snout-vent length; SVL ≥ 100 cm; weight ≥ 200 g) between the months of July through October (window of time when young-of-year (YoY) hatchlings appear on the landscape en masse; see Currylow et al manuscript text) across all years they were encountered (2003–2021) from the Greater Everglades Ecosystem, Florida, USA. During these four months, median sizes for YoY hatchlings were 63.0 cm SVL (interquartile range 58.6–71.5 cm) and 124.6 g (interquartile range = 106.7–194.0 g).
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